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A NEW THEORY FOR THE SENSITIVE PLANT.

Das reizleitende Gewebesystem der Sinnpflanze. By Dr. G. Haberlandt. (Leipzig: W. Engelmann, 1890.)

THE present decade has been a very important one from the point of view of a botanical revival in this country. The seed sown in previous years by Thiselton Dyer and others did not fall entirely on sterile soil, and gradually a school of active workers has arisen, sometimes described, for want of a better name, as "the younger school of botanists." The individuals constituting this "school," though few in numbers, have pursued widely diverging lines of research; some devoting themselves to morphology, others to physiology and minute anatomy, others again to the diseases of plants, &c. Important results have accrued from their labours in the various branches taken up, but in no case have they been more striking than in the field of minute cell anatomy. The readers of this journal hardly need to be reminded that the discovery of the continuity of the protoplasm from cell to cell, and the demonstration of the fact that plant tissues do not consist of a number of isolated masses of protoplasm, cut off from one another by the dead cell-membranes, was largely due to the investigations of Gardiner.

The knowledge of the existence of these uniting filaments seemed from the first to throw light on many intricate and obscure physiological problems. Foremost among these was the possibility that by their instrumentality the transmission of stimuli over considerable tracts might be facilitated. It is interesting to remember that almost the first case of continuity of protoplasm demonstrated by Gardiner was that in the pulvini of the leaves and leaflets of the sensitive plant. Nor did this lose its significance when it was later realized that such a continuity was a very general, if not universal, phenomenon in plant tissues. The view that the stimuli, which undoubtedly travel considerable distances in most of the plants endowed with irritable movements, are transmitted in virtue of these exceedingly fine uniting filaments is one very generally held by botanists in this country, and finds expression in Vines's "Lectures on the Physiology of Plants." Indeed, that this is so, in certain cases, has been experimentally demonstrated. In view of these circumstances, the book whose name heads this review, dealing as it does entirely with the mechanism of stimulus transmission, will be studied with interest, and the more so from the fact that Dr. Haberlandt's "Physiologische Pflanzenanatomie" has done much towards the elucidation of many of the facts of anatomy. Dr. Haberlandt here limits himself solely to the investigation of the means by which a stimulus, set up at some point in the sensitive plant (*Mimosa pudica*), is transmitted to a distance, promoting movements in regions far removed from the point stimulated.

During this century various physiologists have busied themselves with this problem, notably Dutrochet, Pfeffer, and Sachs. The prevalent theory on the Continent, which is associated especially with the name of Pfeffer, briefly amounts to this:—When an irritable portion of one of the pulvini of the sensitive plant is stimulated, the irritable cells lose their turgidity, water passing out of them into the intercellular spaces associated with them; a certain amount of this water is said to enter the tracheides and vessels of the xylem of the vascular bundle, and to upset the hydrostatic equilibrium obtaining there; this disturbance is transmitted to a distance as a wave in the xylem, and stimulates, as it travels along, the irritable cells of the successive pulvini which it passes near, causing them likewise to contract. This may affect merely the pinnules of a single leaf, or, in certain cases, the stimulus may travel from one leaf to another.

This hypothesis is based on very old experiments performed by Dutrochet more than sixty years ago. Dutrochet found that, (1) after the removal of a complete ring or zone of cortical tissue from the stem, a stimulus could still be propagated from one leaf to another, across the decorticated region. A similar result followed when the pith was destroyed, the vascular bundle alone being left intact. The irresistible inference was that the stimulus travelled by the *vascular bundle*. Further, (2) when the woody portion of the bundle was cut into, a drop of liquid was observed to exude immediately, and a stimulus was transmitted upwards and downwards from the point of lesion, causing movements in the nearest leaves and even travelling to more distant ones. The drop which exuded was supposed to come from the wood, and the disturbance of pressure resulting, to initiate the stimulus. Haberlandt deals with this "fundamental experiment," and shows that Dutrochet and the others were in error. To make this clear, it is necessary to briefly indicate the structure of a bundle and adjacent tissues in *Mimosa pudica*. In a transverse section of a stem (and the same holds generally for the petiole) there is externally the epidermis, below which comes the parenchymatous cortex. The cortex passes over into a zone of thick-walled cells, described as collenchyma by Haberlandt, as bast-fibres by some other writers. Within this thick-walled zone is a ring of phloem, and finally the xylems and pith. Dutrochet, when he thought he had dissected away all the tissues outside the xylem in the experiment recorded above (1), had, in point of fact, left not only the phloem, but also the collenchyma-ring intact. His knife had been arrested by the collenchyma, which he had mistaken for the wood. The collenchyma and phloem remained intact, and the inference that the stimulus travelled by the xylem was consequently a false one.

Further, in the case of experiment (2), Haberlandt is at great pains to show that the drops of liquid do not issue from the wood at all, and establishes the fact that they arise in reality from special cells in the phloem. Following the same method of experiment as Dutrochet, Meyen, and Pfeffer, Haberlandt demonstrates clearly—

(1) That the stimulus normally travels inside the collenchyma ring, but outside the xylem of the bundles; in other words, in the phloem.

(2) That, when a stem is cut through, drops exude at the moment of cutting. These drops arise, not from the xylem, but from special cells in the phloem.

This alone marks a considerable advance on the older hypothesis.

Having cleared the ground so far, Haberlandt sets himself two problems for solution, and it is with these that the greater portion of his paper is occupied. These questions are:—

(1) What are the special organs in the phloem which transmit the stimulus?

(2) What are the details of the mechanism of transmission?

As his later inferences and experiments are based on a detailed anatomical study of the sensitive plant, it will be advisable to follow Haberlandt into this matter. The phloem of many Leguminosæ is characterized by the possession of rows of cells, somewhat larger than the true sieve-tubes, which, from the nature of their contents, are known as tannin-sacs. These, in *Mimosa pudica*, are long, tube-like cells, arranged end to end. Each cell possesses a primordial utricle and a large nucleus. The longitudinal walls of these cells are frequently pitted, but the structure of their transverse walls is characteristic. Each possesses a very large, shallow pit. The closing-membrane of the pit is traversed by a number of very delicate protoplasmic filaments. These are much finer than the similar connecting filaments of sieve-tubes, and approximate more nearly to the uniting filaments of adjacent parenchyma cells. Haberlandt shows that it is a portion of the watery content of *these* cells which escapes, when a stem or petiole is cut into; and it is his view that these cells constitute the organs which transmit the stimuli from one point to another in the plant. The watery fluid which exudes from them, usually clear and colourless, gives a very characteristic, and deep reddish-violet colour, with iron chloride, and, if allowed to dry upon a slide, crystallizes out in various forms, usually arranged as sphere crystals or dendritically. This substance is probably of the nature of a glucoside, since, among other reactions, when treated with acids it is broken up into glucose and a resinous body. Accompanying this glucoside is a considerable amount of mucilage.

The distribution of the vascular bundles, in especial relation to these supposed conducting cells, both in leaf and stem, is followed out in detail. The glucoside-containing cells occur, roughly speaking, in two rings in the phloem, one of which is nearer the collenchyma zone, the other nearer the xylem. Some of the former actually touch the collenchyma cells. Where the bundles traverse the pulvini, a much larger proportion of these cells are in contact with the collenchyma. In the leaflets all the larger bundles are accompanied by the glucoside-containing cells, but in the very small anastomoses they die out. Finally, as to the distribution of protoplasmic continuity. This obtains in the soft cortex and in the collenchyma (whose cells are freely pitted). The cells of these two tissue systems are united together by extremely fine filaments in such a manner that an unbroken protoplasmic continuity exists, from the periphery of the pulvinus to the inmost layer of the collenchyma. In the phloem also there exists a similar continuity. Between these two systems, however—the soft cortex and collenchyma on the one hand, and the phloem (including the glucoside cells) on the other—there is, according to Haberlandt, no direct continuity; and although the collenchyma cells are freely pitted on all sides, the closing-membranes of these pits are untraversed by protoplasmic filaments on the side directed towards the phloem (and glucoside cells).

By careful experiments, referred to above, Haberlandt demonstrates (what had been regarded by several observers as probable) that the stimulus travels in the phloem; and in view of the fact that the glucoside sacs emit the drops of liquid on cutting a stem or petiole (thus giving rise to a hydrostatic disturbance), and in view also of inferences drawn from further experiments, to be considered immediately, Haberlandt concludes that the stimuli are transmitted by the rows of glucoside-containing sacs, and this in a purely mechanical manner. Before going on to elaborate his theory, Haberlandt meets and disposes of the hypothesis, mentioned at the commencement of this review, that the stimuli travel from cell to cell by the agency of the uniting filaments of living protoplasm. According to that view, when any pulvinus is stimulated, as by a mechanical shock, its irritable cells contract, losing their turgidity, and a movement results; at the same time the stimulus would be conveyed to the phloem, and there transmitted from cell to cell by the filaments of protoplasm (it is immaterial whether in the phloem-parenchyma, or even in the longitudinally-running series of glucoside sacs) until it reaches another pulvinus, where it would be communicated in the same way to the irritable cells there, and a further movement would result, and so on.

It is necessary at this juncture to explain, so as to make what follows intelligible, that physiologists have availed themselves of two entirely different methods of stimulating the plant—firstly, by submitting a pulvinus to a mechanical shock, without damage to its tissues; and secondly, by cutting the petiole or stem, and causing actual lesion of the conducting tissues. In both cases the stimulus is transmitted, but in the latter to a much greater distance, the method being altogether a more violent one and perhaps quite different in its effects. Pfeffer was content to regard anything of the nature of a "vital" hypothesis of stimulus-transmission as disproved, from the fact that, even when he chloroformed a definite portion of a petiole, a stimulus could still be transmitted through the region subjected to the chloroform. Haberlandt, however, points out that this result must not be taken as final, since there is no proof that the internal tissues had been really acted on by the anæsthetic, as applied by Pfeffer. Further, Vines has pointed out that, although chloroform deprives the *irritable cells of the pulvinus* of their irritability (rendering them rigid), there is no justification for the assumption that it likewise deprives the protoplasm of the *conducting cells* of their conductivity; an objection the validity of which is admitted by Haberlandt. It was necessary, therefore, to make a more crucial experiment to decide this point, and this Haberlandt does by substituting an *actual killing* of the protoplasm in a small portion of a petiole for a mere chloroforming. This was done by steaming a confined zone of a petiole. Under these conditions, the stimulus, to be transmitted successfully, had to pass through a dead region. If the stimulus could be shown to traverse this region, the "vital" hypothesis would be untenable. The result was most instructive. When an ordinary mechanical stimulus was applied, there was no transmission; when, however, a stimulus, caused by a lesion of the tissues, was applied, it was transmitted, in the majority of cases, over the zone previously killed by steam. From this, Haberlandt concludes that no theory which depends on filaments of protoplasm to conduct the stimulus can be maintained. He considers it improbable that a mechanical stimulus and one due to lesion should travel in different ways, notwithstanding the fact, which he mentions later on, that under special conditions a stimulus can be transmitted even by the vessels and tracheides of the xylem. There is nothing surprising in the transmission over a dead region of a stimulus due to lesion. It is just this sort of stimulus that would cause a considerable upset in the hydrostatic equilibrium in the glucoside cells cut into, and it is conceivable that the disturbance due to this sudden fall in pressure might be conveyed, in a purely mechanical manner, over considerable distances. Hitherto it has not been shown that a *normal mechanical stimulus* can be transmitted over a zone that has been rendered incontestably dead.

If the distribution of the continuity of protoplasm in a pulvinus should be, as stated by Haberlandt, such that the outer system of continuous cells extends inwards only so far as, and including, the collenchyma, and that the phloem is independent of this system, then it is difficult to see how the stimulus could pass (by a vital hypothesis) from the irritable and contractile cells to the conducting cells. This result, however, requires confirmation. Gardiner, who investigated the nature of the continuity in these organs of the sensitive plant, makes no comment on any such marked discontinuity of the protoplasm, and the inference, drawn from a study of his paper in the Philosophical Transactions, is that the cells, from the periphery right up to dead vessels of the wood, constitute one connected whole. What he denies to the sensitive plant, Haberlandt admits for other cases. The phenomenon of transmission of stimuli in the stigmas of *Mimulus* and *Martynia*, in the leaves of *Dionæa* and probably of *Drosera*, and in the tendrils of many climbing plants, would seem to be a function of the protoplasmic fibrils. Having dealt with his refutation of the "vital" hypothesis, as applied to the sensitive plant, we may give a short summary of the theory put forward by Haberlandt, though for its details, and the many questions raised therein, the reader is referred to the original text. Haberlandt holds that both in the case of a mechanical stimulus, and in that of one caused by a lesion of the tissues, the transmission is effected in a purely mechanical manner, as a wave or impulse passing along the glucoside-containing cells. Necessarily the transverse walls, which possess each a broad, shallow pit, are regarded as offering little resistance to the filtration of the contained sap. The protoplasm which is continuous through these pit-membranes is not regarded as playing any important part in this event. When a pulvinus is mechanically stimulated, its irritable cells lose water and contract; the disturbance set up by this fluctuation in pressure will start a wave in the rows of conducting cells, travelling from the point at which the increase of pressure occurs. The wave is what may be described as a positive wave (*Bergwelle*), and the method of its transmission is similar to that obtaining in a closed rubber tube distended with water, when it is pinched at one end. This wave, when it reaches the irritable cells of the next pulvinus, will be communicated to them through the elastic collenchyma layer, probably through the pits, which are numerous. In more sluggish cases it may not, perhaps be till an actual *bending* occurs in the stimulated pulvinus that the increase of pressure will be sufficient to start the wave in the conducting cells.

On the other hand, when the stimulus is due to lesion, as when a petiole or internode is cut into with a sharp knife, the wave is set up in a different manner. At the moment of cutting into the turgid, glucoside-containing cells, a drop of liquid escapes, causing a *fall* in pressure. This is transmitted as a negative wave (*Thalwelle*), and will be communicated to the irritable cells at a distance, by the agency of the pits there. In this case, however, the pit-closing membranes of the collenchyma will bulge slightly inwards, in the former case outwards. The communication from the conducting to the contractile cells is rendered easier from the fact that in the pulvinus a much larger proportion of the former lie adjacent to the collenchyma than at other points on the course of the bundle. This special arrangement undoubtedly seems to favour such a theory as that of Haberlandt. Still it must be remembered that it may be due to quite different causes. As is well known, the arrangement of the bundles is always considerably modified at the pulvini, so that the bending may be interfered with as little as possible.

In conclusion, it must be admitted that the paper here reviewed is a masterly piece of work, though, it may be, many naturalists in this country will hardly agree with the author in the inferences which he draws, and the theory which he builds upon them. It must be borne in mind that possibly too important a part may have been assigned to the uniting fibrils of protoplasm as touching the transfer of stimuli of various kinds from cell to cell. In the first blush of a great discovery, of so far-reaching a nature as that of the continuity of protoplasm, and more especially from the fact that at a very early period it was in the sensitive pulvini that this continuity was shown to exist,—in view of this, the position that has been taken up by workers in this country may have been an over-sanguine one. It may be that the explanation of this phenomenon of protoplasmic continuity (though undoubtedly it facilitates transmission of stimuli in certain cases, *e.g.* stigmas of *Mimulus*, &c.) may have another bearing—that it may in some way affect the nutrition of the pit-closing membrane, or even discharge the purely mechanical function of binding the protoplasts to the closing membranes. For the present, although it must be conceded that Haberlandt has considerably advanced our knowledge of this question, in that he has localized the conducting region to the phloem, and has shown that stimuli due to actual lesion can be transmitted in a purely mechanical manner; nevertheless he has failed to demonstrate conclusively the untenability of the "vital" hypothesis in the case of the normal stimulus (*Stossreiz*). This being so, further results must be awaited before this interesting question can be regarded as finally settled.

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